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1Artificial light increases local predator abundance, predation rates, and
2herbivory

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20*urban ecology, species interactions, predation, herbivory, arthropod, insect*

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26 **Abstract**

27 Human activity is rapidly increasing the radiance and geographic extent of
28 artificial light at night (ALAN). The timing and characteristics of light affect
29 the development, behavior, and physiological state of many organisms.

30 Depending on the ecological context, plants and animals respond to artificial
31 lights in both adaptive and maladaptive ways. Mesocosm experiments have
32 demonstrated both top-down and bottom-up control of populations under
33 ALAN, but there have been few community-scale studies that allow for
34 spatial aggregation through positive phototaxis, a common phenomenon
35 among arthropods. We performed a field study to determine the effects of
36 ALAN on arthropod communities, plant traits, and local herbivory and
37 predation rates. We found strong positive phototaxis in 10 orders of
38 arthropods, with increased (159% higher) overall arthropod abundance
39 under ALAN compared to unlit controls. The arthropod community under
40 ALAN was more diverse and contained a higher proportion of predaceous
41 arthropods (15% vs 8%). Predation of immobilized flies occurred more 3.6
42 times faster under ALAN; this effect was not observed during the day.

43 Contrary to expectations, we also observed a 6% increase in herbivory under
44 ALAN. Our results highlight the importance of open experimental field studies
45 for determining the community-level effects of ALAN.

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53 **Introduction**

54 Terrestrial organisms nearly ubiquitously use light to gather
55 information about their environment, with most taxa capable of responses to
56 changes in spectral composition, intensity, or duration (Cashmore et al.
57 1999). Humans frequently modify the light environment in the increasingly
58 broad spaces in which we live and work, with light emittance increasing 2.2%
59 annually worldwide between 2012 and 2016 (Kyba et al. 2017). Light
60 emittance will likely continue to increase as LED's lower the cost of installing
61 and operating lights globally (Pust et al. 2015).

62 One of the most noticeable effects of artificial light at night (ALAN) is
63 movement toward light sources by arthropods (positive phototaxis) and has
64 been a subject of study for many decades. Positive phototaxis can locally
65 increase the abundance of an arthropod species 20-fold (Eccard et al. 2018),
66 but the opposite effect, negative phototaxis (repellence) is also frequently
67 observed (Owens and Lewis 2018). There have been only a limited number
68 of studies that compare phototaxis within communities of arthropods, and
69 even fewer describing changes in local composition as it relates to trophic

70strategy or other life history correlates (Gaston et al. 2015). Even if all
71nocturnal arthropods were uniformly attracted, nocturnal arthropods are on
72average larger compared to diurnal communities in the same location and
73have different trophic strategies (Guevara and Avilés 2013, McMunn and
74Hernandez 2018). ALAN could lead to “nocturnal enrichment”, a local
75aggregation of animals biased toward nocturnally active taxa. Nocturnal
76enrichment would lead to larger average body sizes and differing prevalence
77of trophic strategies in areas exposed to ALAN. Beyond phototaxis, there are
78many other ways in which ALAN can directly affect arthropods, with
79examples of spatial and temporal disorientation, desensitization to light, and
80changes in pattern recognition ability (Owens and Lewis 2018). These direct
81effects of ALAN on arthropods can be specific on the basis of size (Heiling
82and Herberstein 1999), developmental stage (Durrant et al. 2018), or sex
83(van Geffen et al. 2014).

84 Plants, like arthropods, have a diversity of responses to ALAN. Light is
85perhaps most obviously used for photosynthesis among plants, but
86photoperiod and spectral composition also serve as important daily and
87seasonal cues. Artificial lights are often bright enough to affect plant
88physiology (Briggs 2006), phenology (Bennie et al. 2016), form, and resource
89allocation (Bennie et al. 2016). Earlier or later phenologies, increased or
90suppressed growth (Cathey and Campbell 1975), decreased flower
91production (Bennie et al. 2015), and altered leaf toughness (Grenis and
92Murphy 2018) have all been observed as direct plant responses to ALAN.

93 While there is an abundance of previous research on responses of
94 individual species to ALAN, there is comparatively less work characterizing
95 how artificial lights affect the composition of ecological communities and
96 species interactions. However, several studies have described how nocturnal
97 predators exploit aggregations of prey items around light sources. For
98 example, bats have increased capture success of moths under lights, not
99 only to due to increased local moth abundance, but also moth disorientation
100 and diminished predator avoidance behaviors (Rydell 1992, Acharya and
101 Fenton 1999). Among web-building spiders, ALAN increases prey catch, with
102 illuminated sites being preferred and occupied by larger spiders (Heiling and
103 Herberstein 1999). Changes in activity time of local fauna can also affect
104 predator abundance, with diurnal cursorial spiders capable of extending
105 foraging duration under ALAN (Peckhamia 2009)
106. Increased predator abundances near light sources and other costs of
107 phototaxis presumably reduce moth fitness when lights are common, with
108 selection leading naïve urban moths to display reduced phototaxis compared
109 to their rural counterparts (Altermatt and Ebert 2016).

110 There are substantially fewer studies that have investigated how
111 artificial lights affect plant-arthropod interactions. Previous studies have
112 shown that plants can have tougher leaves under ALAN, reducing herbivore
113 performance (Grenis and Murphy 2018). Similarly, a mesocosm experiment
114 documented bottom-up control of an aphid population, with the outcome
115 affected by the type of light source used (Bennie et al. 2015). There are

116likely negative impacts for plants dependent on nocturnal pollination
117services under ALAN, as these pollinators may be reduced in effectiveness or
118population size (Macgregor et al. 2014, Knop et al. 2017). Finally, defensive
119traits of plants can be under circadian regulation (Goodspeed et al. 2012)
120and ALAN could alter the timing of expression of these traits.

121 The effects of ALAN may modify local population sizes, through either
122top-down or bottom-up regulation, but little is known about the relative
123strength of artificial light effects on these two mechanisms. In one study,
124parasitoid wasps exerted top-down control of an aphid population under
125ALAN, with maximum effectiveness at low light intensity (Sanders et al.
1262018). A second study described bottom-up effects on aphid populations,
127regulated through flower head density, and with effect size corresponding to
128the type of artificial light source used (Bennie et al. 2015). However, it is
129unclear if these effects would persist in open communities, as closed
130mesocosm studies do not allow for the immigration, emigration, or short-
131term movement of predators or herbivores. Open experiments that allow for
132the combined effects of altered behavior and altered local composition are
133rare (Sanders and Gaston 2018). In one of the few studies on the topic at the
134ecosystem scale, ALAN modified riparian-terrestrial nutrient fluxes over the
135course of a year (Meyer and Sullivan 2013), suggesting that the effects of
136ALAN can scale up to significantly alter ecosystem function.

137 Studies that investigate how artificial light alters local community
138composition and species interactions will be necessary to fill the current gap

139in knowledge at population and community scales. Artificial light may alter
140community interactions through a variety of mechanisms including effects on
141plant tissue quality or quantity, herbivore abundance or behavior, or
142predator abundance or behavior. Here, we ask how artificial light affects
143arthropod communities, plant traits, herbivory, and predation. To
144characterize these effects, we conducted an open field experiment using
145artificial lights to assess changes in the activity-abundance and traits of
146arthropod communities under ALAN, as well as changes in local rates of
147herbivory and predation. We predicted that artificial lights would increase
148the local density of predators in the community, leading to stronger top-
149down regulation of herbivores and a decrease in herbivory under artificial
150lights. This *“over-compensatory predation”* hypothesis predicts that
151predators would aggregate in lit plots in response to allochthonous prey
152subsidies at night and would continue to exert consumptive or non-
153consumptive negative effects on herbivores during the day, decreasing
154overall herbivory. Alternatively, if artificial lights attracted herbivores more
155strongly than predators, local increases in herbivore pressure could result in
156an increase in total herbivore damage. This *“increased herbivory”* hypothesis
157would be supported if the responses of predatory taxa were unable to
158compensate for light-mediated increases in herbivore activity or abundance.

159**Methods**

160*Summary*

161 We monitored local mobile arthropod abundance, growth and
162 herbivory of three plant species, and assayed predation rates under two
163 experimental treatments - artificial light at night "ALAN" and an
164 unilluminated control. All analyses were performed in R (version 3.5.1) (R
165 Core Team 2017) and all plots were created with *ggplot2* and *ggmap*
166 (Wickham 2009, Kahle and Wickham 2013).

167 *Experimental light treatments*

168 We illuminated plants and insect traps with artificial light at night,
169 while others remained unilluminated as a control. We used tomato cages (65
170 cm tall) as a scaffold for each replicate onto which we mounted LED's, white
171 plastic bowls to reflect light downward, white plastic sheets to reflect light
172 laterally, and sticky traps. Each replicate was randomly assigned one of
173 three experimental treatments: 1) no artificial light, 2) artificial at night, or 3)
174 artificial at night with periodic spider removal. LED lights were directed
175 downward (12V, 3 diodes each, FlexFire Outdoor (IP65) UltraBright™ Design
176 Series LED Strip Light 4200K - Natural White) and were mounted
177 approximately 55 cm above the ground inside an overturned white plastic
178 bowl (Figure 1). This apparatus resulted in lighting similar to the intensity
179 and wavelengths beneath LED streetlights (Bennie et al. 2016), providing an
180 nighttime illuminance of 749 lux at 50 cm, 167 lux at 10 cm, and 76.5 lux at
181 ground level for ALAN treatments. The distance between plots was sufficient
182 to isolate our lighting manipulation; adjacent control replicates had no
183 measurable incidental lighting, with 0 lux at all heights. LED strips were

184wired in parallel using 14 gauge wire, and circuits were designed to minimize
185voltage drop along the length of wire and minimize the amount of total wire
186used, resulting in 4-6 circuits in each block (Supplemental Figure 1). Within
187blocks, plots were arranged in a grid with 3m spacing (Figure 2).

188*Field site*

189 We conducted the study within the University of California Putah Creek
190Reserve Experimental Ecosystem (Davis, CA, USA 38° 31.76'N, 121°
19148.48'W). There are abundant invasive and native grasses and bunchgrasses
192(Poaceae) across most of the area with small stands of eucalyptus
193(*Eucalyptus* sp.), oak (*Quercus* spp.), walnut (*Juglans* sp.), almond (*Prunus*
194sp.), cottonwood (*Populus fremontii*), and dogwood (*Cornus* sp.) dispersed
195throughout. Putah Creek flows along the southern boundary of the site.

196 Blocks differed in terms of local vegetation and management history
197(Figure 2). The “basin” block (38° 31.757'N, 121° 48.556'W) was established
198in a long-abandoned water retention pond dominated by non-native forbs
199and grasses (*Centaurea* sp., *Silybum* sp., *Rumex* sp., and *Avena* sp.). The
200“grassland” block (38° 31.759'N, 121° 48.482'W) was established in a
201seasonally mowed grassland dominated by native and non-native grasses
202(*Elymus triticoides*, *Stipa pulchra*, *Avena* sp., and *Bromus* sp.). The “riparian”
203block (38° 31.686'N, 121° 48.453'W) was established in a restored
204grassland, approximately 30m from Putah Creek with a wider variety of
205herbaceous species (including *Vicia* spp., *Brassica* sp., *Avena* sp., *Elymus*
206*triticoides*, *Stipa pulchra*).

207 An empty 530 mL cup (SOLO brand) was installed beneath each plot
208 and served as an epigeal live trap. This pitfall trap was filled with dead grass
209 to allow arthropod escape in all but ALAN spider removal replicates, in which
210 case traps were cleared of spiders every 48 hours. Experimental data were
211 initially analyzed separately for the two illuminated treatments (ALAN and
212 ALAN with periodic cursorial spider removal). However, nearly all response
213 variables, including cursorial spider abundance, did not differ between the
214 two treatments. The only response variables that differed between these two
215 treatments were taxon-specific arthropod abundances; Lithobiomorpha,
216 Spirobolida, Isopoda, and the family Hymenoptera-Formicidae were all
217 reduced in abundance in the ALAN spider removal treatments compared to
218 the ALAN treatments, but both illuminated treatments were elevated
219 compared to control treatments. Due to the ineffectiveness of our attempts
220 to remove spiders, these two treatments, ALAN and ALAN with spider
221 removal (60 replicates total) were combined, hereafter simply referred to as
222 “ALAN” and compared to 30 replicates that were unilluminated “control”.

223 *Plantings*

224 We grew *Brassica nigra* and *Pisum sativum* seedlings in Ray Leach
225 Cone-tainers (SC7 Stubby 3.8 cm dia, 14 cm depth, 107 ml vol, Stuewe &
226 Sons Inc.) and obtained starts of a third species, *Solanum lycopersicum*. We
227 transplanted 270 seedlings from the greenhouse into pre-dibbled holes
228 underneath tomato cages, split among three blocks (30 replicates per block,
229 each replicate with all 3 species of plants). Plants were at a median height of

23010.2 cm at the time of transplants. The experiment was repeated with three
231cohorts of plants, transplanted into the field April 11, April 25, and May 9,
2322017. Plants were surveyed for leaf number, number of leaves with insect
233damage, estimated area, estimated area damaged, height, and status (alive/
234dead) initially and after one week of experimental treatments. The second
235cohort of plants experienced very high drought-induced mortality due to an
236early-season heatwave and we excluded this cohort from all analyses of
237plant traits. To test hypotheses for direct effects of ALAN on plant size we
238applied likelihood ratio tests to linear models of plant height and plant area,
239each including fixed effects for treatment, cohort, block, and species. To
240determine if herbivory differed under ALAN, we applied a likelihood ratio test
241to a beta distribution glm (*package* betareg 3.1) of proportion damaged
242leaves (exact 0's and 1's transformed to 0.001 and 0.999 respectively). This
243model included fixed effects for treatment, cohort, block, and species. To
244determine if ALAN affected plant survival, we applied a likelihood ratio test to
245binomial GLM fit to plant status (live/dead) including fixed effects for
246treatment, cohort, block, and species.

247*Arthropod collection and web counts*

248 We monitored arthropods weekly at each of the 90 replicates using 24-
249hour pitfall traps (530 mL cup, filled with 100 mL dilute detergent) and 48-
250hour sticky traps (10 cm x 20 cm translucent overhead projector sheets with
251both sides coated in Tanglefoot Sticky Barrier (The Scotts Company LLC). We
252identified individuals to order and measured body length excluding antennae

253and appendages. All arthropods <1 mm length (mostly Collembela) were
254excluded from samples. We extended order-level identification to subdivide
255Hymenoptera into bees, ants, and wasps as well as separating the sub-order
256Homoptera from all other Hemipterans. Orders in which a large majority of
257taxa are known to have the potential to act as predators: Aranea,
258Dermaptera, Lithobiomorpha, Neuroptera, and Opiliones, were counted as
259predators. Several frequently observed and easily identified families of
260predatory arthropods were also counted as predators (Carabidae -
261Coleoptera, Asyllidae - Diptera, Reduviidae - Hemiptera, and wasps of any
262taxa larger than 10 mm). All other arthropods were counted as non-
263predators. We aimed to capture all potential predators in our classification,
264regardless of primary trophic strategy. In particular, earwigs (Dermaptera),
265were counted as predators, and were observed acting both as nocturnal
266herbivores (Strauss et al. 2009) and consuming subdued flies. Counts of
267predator/non-predator separated by order and collection method are
268reported in Supplemental Figure 2.

269 To test for differences in the abundance of individual arthropod taxa
270between treatments we utilized the R function `many.glm()`, which accounts
271for multiple hypothesis testing of taxa abundance, and used a negative
272binomial error distribution and estimated a fixed effect for treatment (R
273package *mvabund* 3.13.1) (Wang et al. 2012). To determine if arthropod
274communities differed in either alpha or Shannon diversity underneath
275artificial light, we used ANOVAs including fixed effects for treatment, block,

276and cohort. To test the hypothesis that artificial light altered overall
277abundance of arthropods we applied a likelihood ratio test to a negative
278binomial GLM (glm.nb - package MASS 7.3) including fixed effects for
279treatment, block, and cohort. To determine if arthropods under artificial light
280were more frequently predaceous we applied likelihood-ratio test to a GLM
281with a beta distribution describing proportion predaceous (exact 0's and 1's
282transformed to 0.001 and 0.999) as a function of treatment, block and
283cohort. Finally, to test for differences in body size between treatments, we
284utilized a Kolmogorov-Smirnoff tests between arthropods collected under
285ALAN and control treatments.

286 We counted volunteer spider webs on each replicate during the day,
287every 48 hours, but the Tetragnathid spiders that were common at this site
288consume their web each morning, and thus our repeated daytime counts
289were too low for statistical analysis. To accommodate this life history, we
290surveyed all replicates for spider webs on tomato cages on two nights, May
29111, 2017 (riparian block only) and May 17, 2017 (all blocks) from 22:20-
29200:20. Only nocturnal web counts are reported. We modeled spider-web
293presence/absence as a function of light treatment using a binomial
294generalized linear model with block and cohort fixed effects.

295*Predation Assay*

296 We measured the rate of predation of immobilized *Drosophila*
297*melanogaster* individuals at each plot separately during the day and the
298night on May 11, 2017. For each plot, we anesthetized 5 *Drosophila*

299 *melanogaster* individuals using carbon dioxide and glued their wings to a
300 small wooden dowel (Elmer's glue - 3.15 mm diameter dowel). We placed 5
301 living dowel-mounted flies on the ground, tucked under the edge of each
302 tomato cage, from 13:50-15:50 (day) and again from 22:20-00:20 (night). We
303 counted the number of flies remaining on the dowel after 2 hours and
304 modeled rate of predation as a function of treatment using a binomial
305 generalized linear model with a block fixed-effect, with separate analyses for
306 day and night data.

307 **Results**

308 *Arthropod community*

309 We collected, measured, and identified a total of 60,180 arthropods.
310 Artificial light at night dramatically altered the arthropod community, with
311 arthropod overall abundance 159% higher across ALAN replicates
312 ($\chi^2(1)=129.44$, $p<0.001$) (Figure 3a) and 8 orders demonstrating strong
313 positive phototaxis (Aranea: 459% increase, Coleoptera: 54% increase,
314 Dermaptera: 2075% increase, Diptera: 335% increase, Isopoda: 270%
315 increase, Lepidoptera: 375% increase, Lithobiomorpha: 465% increase,
316 Opiliones: 1120% increase, Orthoptera: 613% increase, Trichoptera: 1027%
317 increase, all p-values < 0.007) (Figure 4, Supplemental Table 1 - model
318 summary statistics). We found no orders demonstrating significant negative
319 phototaxis.

320 The effect of phototaxis on arthropod overall abundance (percent
321 increase in arthropod abundance in ALAN treatments) was larger in sticky

322traps compared with pitfall traps (interaction effect, $\chi^2(1)= 16.7$, $p<0.001$)
323(157% increase in sticky trap, 427% increase in pitfall trap). These effects
324also differed by block ($\chi^2(2)= 27.7$, $p<0.001$,) (365% increase in riparian,
32558% increase in basin, 59% increase in grassland) and cohort ($p<0.001$,
326 $\chi^2(2)= 13.6$) (54% increase in cohort 1, 227% increase in cohort 2, 59%
327increase in cohort 3). Notably, a fly emergence during cohort 2 at the
328Riparian site contributed a great deal to these treatment interactions. In our
329nocturnal web survey, spider web occurrence was more common on
330artificially lit plants ($\chi^2(1)= 3.78$, $p<0.05$, 36% ALAN treatment with webs,
33120% control with webs) (Figure 4).

332 Arthropod composition varied significantly between ALAN and control
333replicates (PERMANOVA, $p<0.001$, $F(1) = 29.12$, $R^2 = 0.05$) (Figure 3e) as
334well as between blocks ($p<0.001$, $F(2)=5.24$, $R^2 = 0.02$) and cohorts
335($p<0.001$, $F(2)=19.63$, $R^2 = 0.07$). We found higher alpha diversity in the
336ALAN treatment ($p<0.001$, $F(1)= 56.77$), but no difference in Shannon
337diversity ($p<0.95$, $F(1)= 0.00$) (Figure 3b and c). We found a higher
338proportion of predaceous arthropods in the ALAN treatment ($p<0.001$, $\chi^2(1)=$
339= 13.72, 16% predator ALAN, 8% predator control) (Figure 3d).

340 Many of the commonly collected orders differed in body size
341distribution collected under ALAN: Aranea ($p<0.001$, $D = 0.20$), Coleoptera
342($p<0.001$, $D = 0.31$), Diptera ($p<0.001$, $D = 0.07$), Hemiptera
343(Homopterans) ($p<0.009$, $D = 0.10$), Hemiptera (non-Homopterans)
344($p<0.002$, $D = 0.12$), Lepidoptera ($p<0.02$, $D=0.55$), Orthoptera ($p<0.02$,

3450.35), and Trichoptera ($p < 0.001$, $D = 0.78$) (Supplemental Figures 3-10). All
346 significant orders contained larger mean size of individuals under ALAN
347 treatments with the exception of Hemipterans (Homopteran and non-
348 Homopteran), which were on average smaller under ALAN.

349 *Plant size and herbivory*

350 We found no evidence of direct effects of ALAN on plant height
351 ($p < 0.24$, $F(1) = 1.37$), plant area ($p < 0.58$, $F(1) = 0.30$), or survival ($p < 0.62$,
352 $\chi^2(1) = 0.25$). We found a small indirect negative effect on plants under ALAN,
353 with a higher proportion of leaves damaged by herbivores ($p < 0.016$,
354 $\chi^2(1) = 5.83$: 34.6% leaves damaged in ALAN treatments, 28.6% leaves
355 damaged in control) (Figure 5). A similar trend was found with percent area
356 damaged, though not statistically significant ($p < 0.366$, $\chi^2(1) = 0.82$: 9.5%
357 area damaged ALAN, 8% area damaged control). When species were
358 separated for analysis, tomato and brassica demonstrated an elevated
359 proportion of leaves damaged (tomato: $p < 0.026$, $\chi^2(1) = 4.93$, brassica:
360 $p < 0.050$, $\chi^2(1) = 3.83$).

361 *Predation experiment*

362 We found increased fly predation rates at night under artificial light
363 treatments ($p < 0.001$, $\chi^2(1) = 63.16$, 3.65 times higher predation rates under
364 ALAN) but found no difference in predation rates between treatments during
365 the day ($p < 0.947$, $\chi^2(1) = 0.04$) (Figure 6).

366 **Discussion**

367 ALAN dramatically altered arthropod abundance and composition in
368our experiment leading to a more diverse and predator-biased community.
369We found higher rates of predation on immobilized flies under ALAN at night,
370but not during the day. We found no direct effects of ALAN on plant size or
371survival but did find a small increase in the rate of herbivory. Our study
372found slightly larger individuals from several orders under ALAN.

373 Our results reinforce the importance of predator aggregation near light
374sources, with nearly double the proportion (15% vs 8%) of the community
375identified as predators under ALAN. Our predation experiment suggests that
376these predators are active or present primarily at night, as we saw no
377difference in predation rates between treatments during the day, but
378nighttime predation increased by 3.65 times. Previous results suggest that
379naïve web-building spiders prefer illuminated portions of a prey-free lab
380habitat, suggesting some portion of predatory taxa may be responding to the
381light source directly rather than a local aggregation of prey items (Heiling
3821999). Finally, spiders have been shown to remain in prey-rich areas longer
383(Olive 1982, Bradley 1993), a distinct mechanism from phototaxis that we
384cannot rule out. Future studies should separate collection of arthropods
385between day and night collections, which could help identify attraction vs.
386retention as the mechanism of predator enrichment.

387 The observed increase in herbivory was unexpected given the
388increased abundance of predaceous arthropods. The increase in the
389proportion of leaves damaged by herbivory could be driven by changes in

390plant traits, herbivore abundance, or herbivore behavior. For example, this
391pattern could emerge if plants under light were less defended and therefore
392more palatable compared to other local plants. However, a previous no-
393choice feeding experiment suggested that exposure to artificial lights
394increased the toughness of smooth brome (*Bromus inermis*) (Grenis and
395Murphy 2018). The increase in herbivory observed in our study would require
396that artificial lights changed plant traits in ways that increased their
397susceptibility or attractiveness to herbivores. Artificial light could have
398caused an increase in local abundance of herbivores or an increase in the
399time that local herbivores spend feeding; these changes could result from
400the direct effects of ALAN on herbivores themselves, or they could result if
401resident predators were effectively satiated by light-mediated allochthonous
402prey subsidies at night, leading to reduced top-down effects on local
403herbivores. An increase in herbivory also occur if the observed increase in
404predatory taxa actually included important plant-feeding omnivores as well.
405This explanation is consistent with our observations of European earwigs
406(*Forficula auricularia*) feeding aggressively on plants at night (Strauss et al.
4072009).

408 Our observation that several orders were represented by larger
409individuals in ALAN treatments is consistent with previous findings that on
410average, orders are represented by larger individuals at night (Guevara and
411Avilés 2013, McMunn and Hernandez 2018). Several non-exclusive
412mechanisms that could explain this pattern are: 1) nocturnal arthropods

413 move toward ALAN more frequently than diurnal arthropods or 2) nocturnal
414 arthropods persist in the vicinity of ALAN longer than diurnal arthropods
415 (Davies et al. 2012, 2017) or 3) larger individuals compete more effectively
416 for high-value ALAN territory (Heiling and Herberstein 1999).

417 Our experimental results suggest that predation and herbivory happen
418 more frequently under ALAN. The magnitude of the increase in nighttime
419 predation was much larger than the increase in overall herbivory (265% vs
420 6%), suggesting that ALAN may generally favor predaceous arthropods by
421 aggregating and disorienting prey items (Acharya and Fenton 1999). Future
422 studies should investigate whether this increased intensity of species
423 interactions results in more total instances of herbivory or predation over the
424 landscape or whether the occurrence of interactions is spatially or temporally
425 aggregated. To quantify landscape level effects of ALAN, a regional
426 unilluminated control should be utilized, to determine baseline rates of
427 predation and herbivory compared to local control plots that may be drained
428 of arthropods by ALAN. This approach, if performed at the appropriate spatial
429 scale, could quantify the likely small decrease in arthropod abundance and
430 species interactions in the broad areas surrounding lights. Our study further
431 reinforces the importance of better understanding the spatial and temporal
432 scales over which ALAN effects community and ecosystem processes (Perkin
433 et al. 2011, Gaston et al. 2013). It has been suggested that one of the most
434 palatable ways to mitigate impacts of ALAN on natural systems may be to
435 strategically limit duration (Gaston et al. 2012), but the effectiveness of this

436method depends on the yet unmeasured speed of discovery and
437abandonment of ALAN sites by arthropods.

438 Finally we suggest future work to explore the interaction of ALAN with
439seasonal and daily temperature variation (Sanders and Gaston 2018).
440Climate change has led insects to shift seasonal and geographic ranges
441tracking beneficial thermal windows. The extent to which currently diurnal
442arthropods are capable of nighttime activity depends on other traits, in
443particular visual acuity in low light, but as organisms track a thermal window
444of activity, a portion of historically diurnal or crepuscular species may shift a
445portion of their activity to the night (Levy et al. 2018) and encounter effects
446of ALAN more frequently. This interaction between ALAN and climate change
447could be exacerbated by diurnally asymmetric warming, with nighttime
448temperatures warming more dramatically than daytime temperatures (Karl
449et al. 1991).

450 We demonstrate that differences in relative phototaxis of arthropods
451leads to dramatic changes in local community composition. This effect of
452aggregation is stronger among predators, and we see a corresponding large
453increase in the rate at which subdued prey are taken beneath ALAN. The
454effects of ALAN within communities are dramatic and complex and yet poorly
455understood. Further research, especially experiments allowing for local
456aggregation of arthropods, is needed to understand and mitigate impacts of
457ALAN on arthropod populations.

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465us with flies, and Jared Reynberry for generously providing tomato starts.

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474**Figure 1.** Schematic diagrams and photo of the apparatus used for each plot
475in this experiment (a-b). Each apparatus consisted of a tomato cage
476structure with a LED light strip affixed at the top. A white plastic bowl was
477used to direct the light downward onto a white plastic reflector and a slightly
478larger transparent acetate sticky sheet. Both sheets were suspended
479vertically with nylon monofilament line. A pitfall trap with a rain cover was
480established at the center of each plots, and three species of seedling plants

481 were installed in the ground around the pitfall trap during each sampling
482 period. c) An image of an illuminated apparatus at night.

483 **Figure 2.** a) Map of experimental blocks used in this study. b-d) Each block
484 consisted of 30 plots arranged in a 3m grid with randomized treatment
485 assignments. White-filled points represent plots illuminated at night, and
486 black-filled points represent plots that were not illuminated.

487 **Figure 3** - Arthropod community summary statistics separated by treatment
488 (ALAN and control) combined from pitfall (24-hour) and sticky traps (48-hour)
489 (a-d) mean values per sample \pm 1 standard error) a) total arthropod
490 abundance b) arthropod alpha diversity per sample C) arthropod Shannon
491 diversity per sample D) proportion arthropods sample assigned to predator
492 category E) NMDS projection of arthropod community by treatment.

493 **Figure 4** - Arthropod taxa displaying significant phototactic response. Panels
494 separated by order and displaying mean abundance by treatment (ALAN vs.
495 control) per sample \pm 1 standard error from the total of pitfall (24-hour)
496 and sticky (48-hour) traps. We found no examples of negative phototaxis.
497 The degree of positive phototaxis displayed by orders varied by over an
498 order of magnitude across taxa.

499 **Figure 5** - Mean proportion leaves damaged by treatment \pm 1 standard
500 error a) mean proportion leaves damaged across all plant species b) mean
501 proportion leaves damaged - tomato only c) mean proportion leaves
502 damaged - brassica only d) mean proportion leaves damaged - pea only. We

503found a modest increase in the proportion of leaves receiving herbivory in
504response to ALAN overall, among tomatoes, and among peas.

505**Figure 6** - Mean proportion of flies eaten in predation assay +/- 1 standard
506error under ALAN and control replicates a) daytime assay (2 hours) b)
507nighttime assay (2 hours). We found a dramatic increase in nocturnal
508predation rates under ALAN but saw no difference in daytime predation
509under ALAN treatments.

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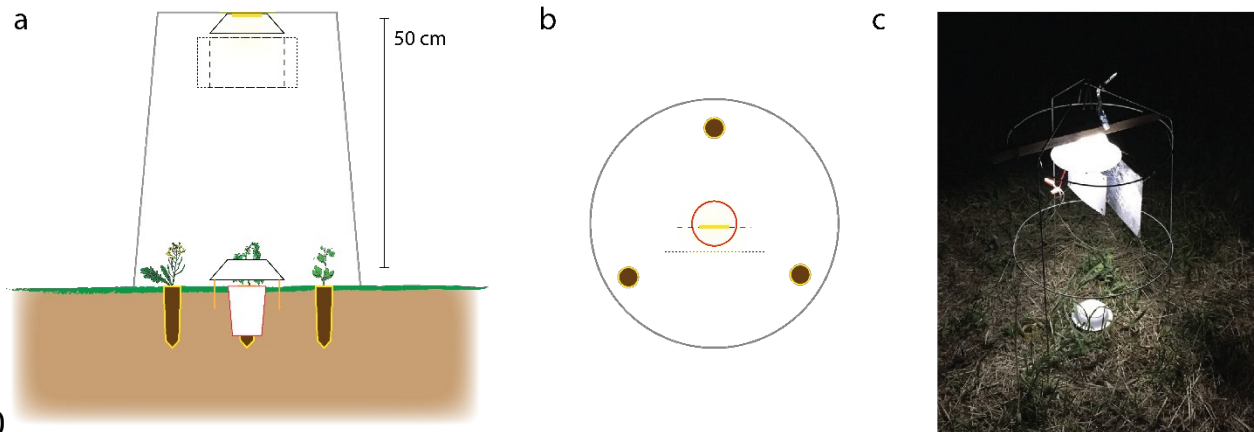
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527 **Figure 1 - experiment schematic**

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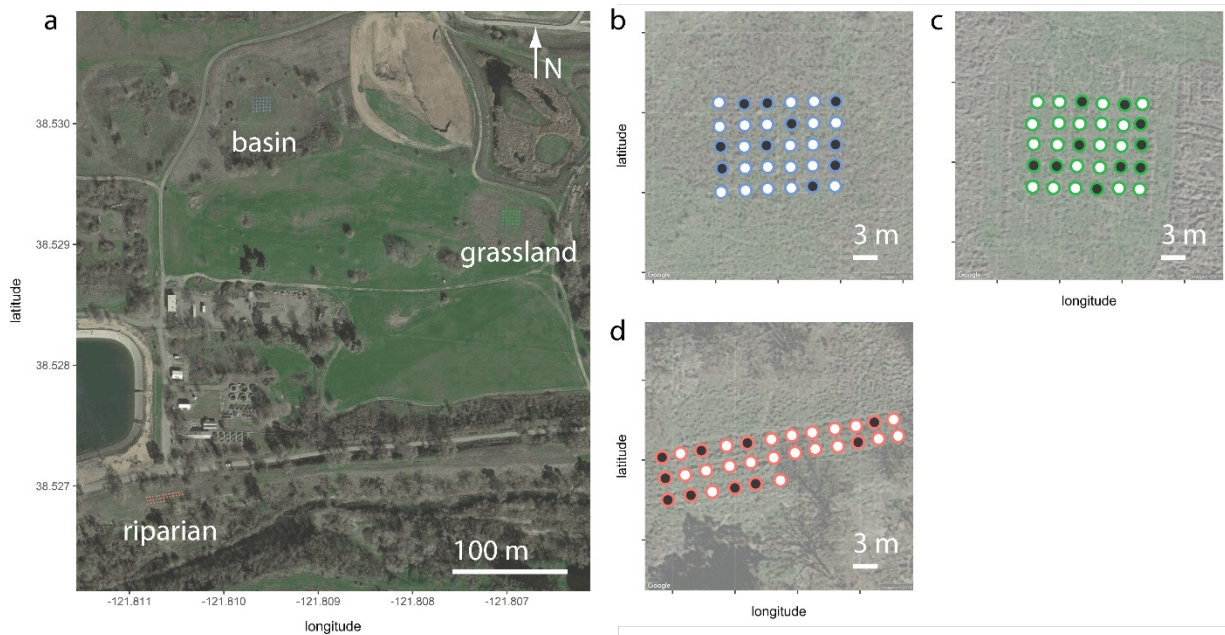
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545 **Figure 2**



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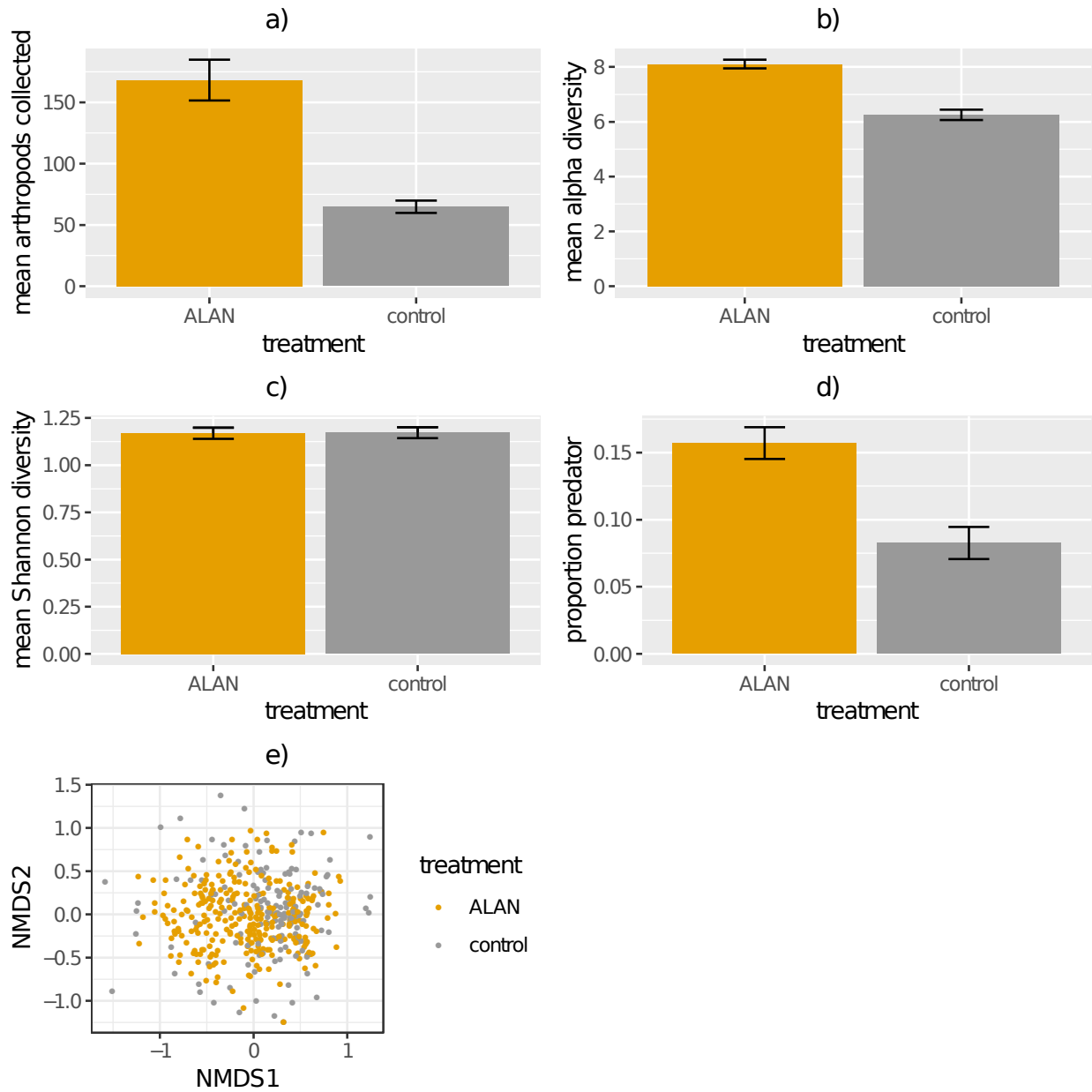
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560 **Figure 3**



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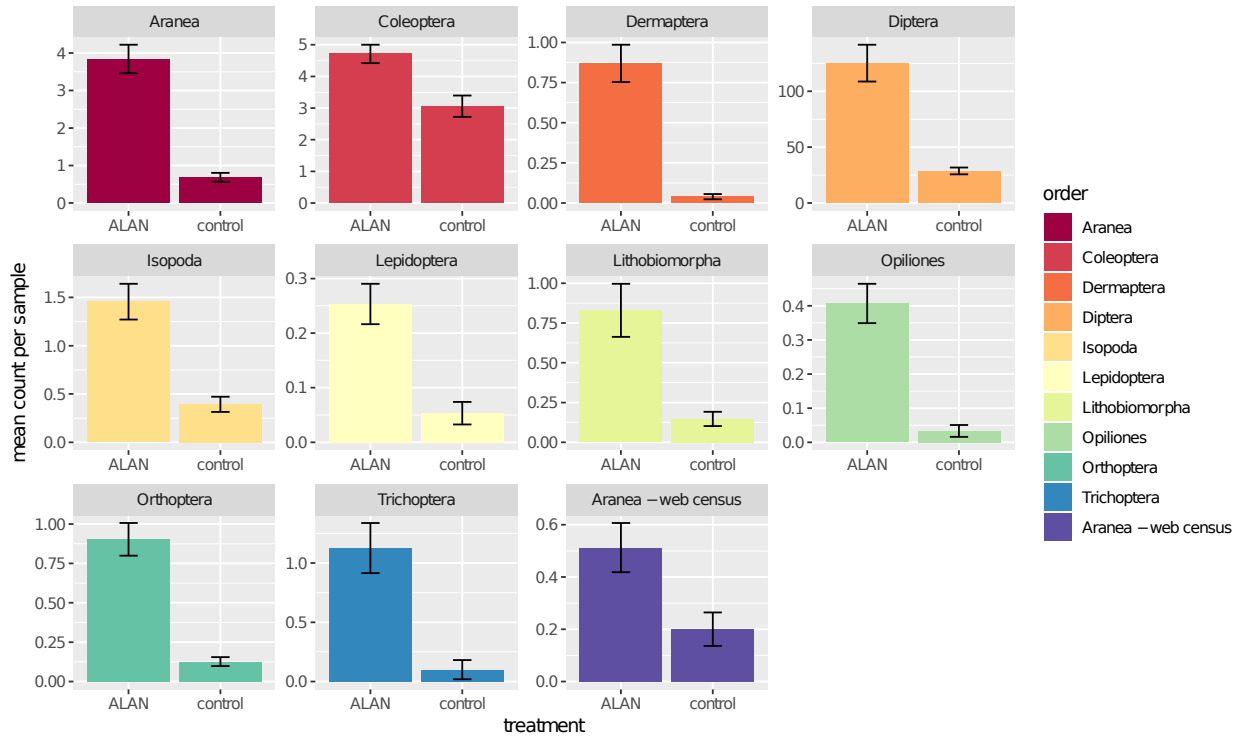
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567 **Figure 4**



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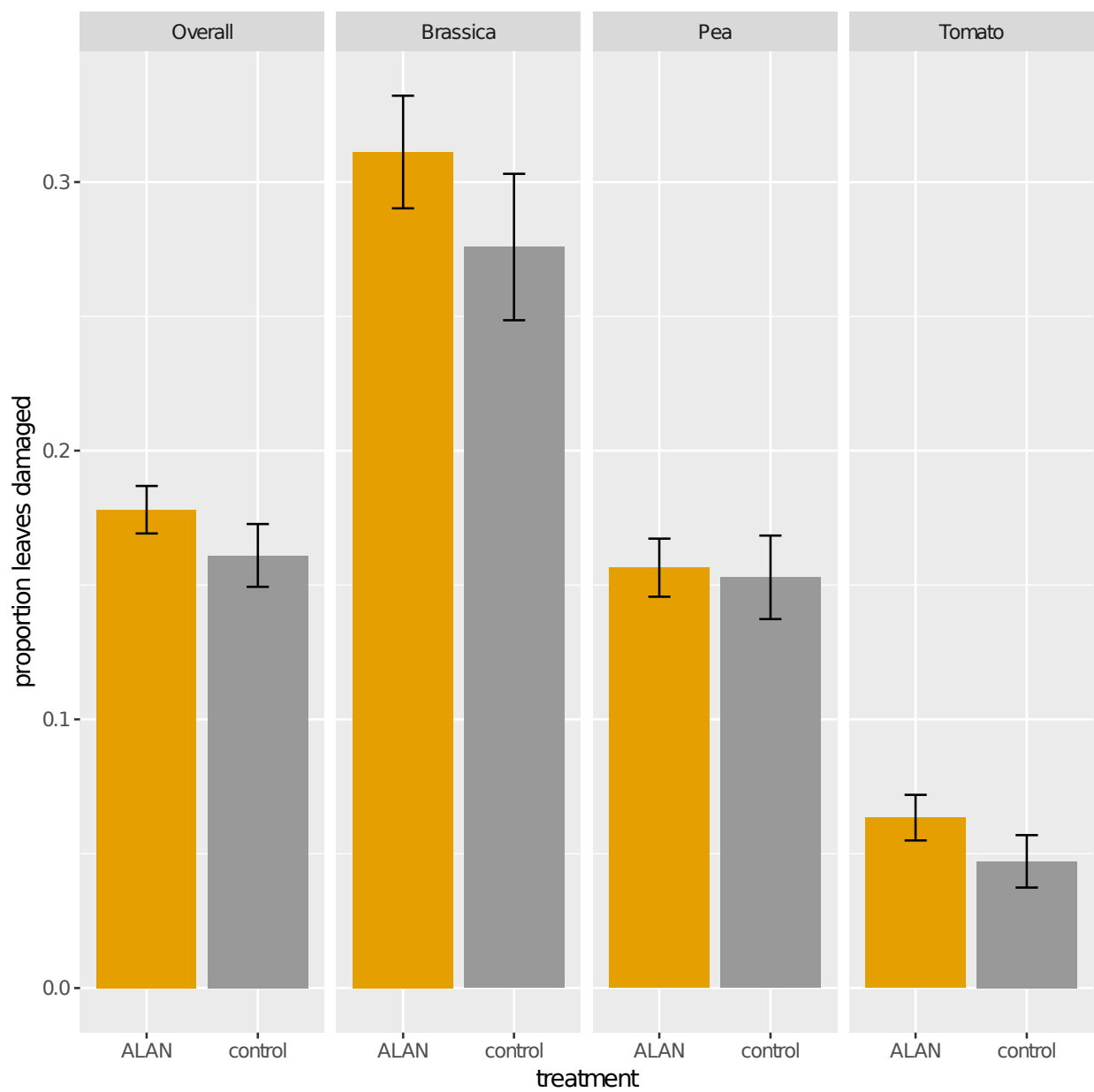
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581 **Figure 5**



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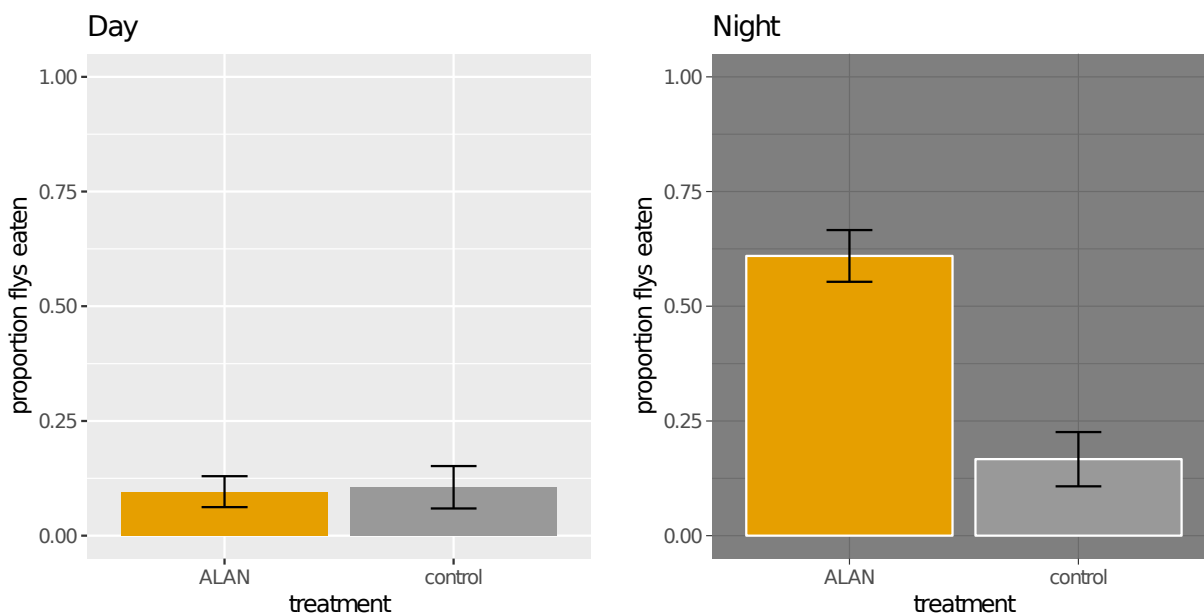
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588 **Figure 6 - predation experiment**



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